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Foraging areas and relative density of bats (Chiroptera) in differently human transformed landscapes

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Abstract

This study on the foraging areas of bats was conducted on 64 transects (2 km long) in different habitats and urban zones in central Poland. Relative bat densities in the city (Warsaw) were only slightly lower than in comparable habitats outside the city. The maximum densities of foraging bats were noted in wooded and riparian habitats (in the city respectively 2.0 and 1.0 records/100 m per count; outside of the city – 1.8 and 1.5 records/100 m per count). Open areas were the least frequently visited by foraging bats. Built-up areas outside the city were characterized by higher densities than city built-up areas. The percent of *Eptesicus serotinus* records was highest in the central zone (about 66%) and decreased with the distance from the city centre. The main foraging areas of *Nyctalus noctula* were distributed in riparian habitats of all zones. *Pipistrellus nathusii* and *Myotis* spp. were more frequent in a landscape less transformed by human activity. Tree cover within a foraging site was the most important factor influencing bat density.

Key words: Chiroptera, foraging, habitat use, urbanization, Poland

Introduction

Most European bat species are synanthropic, frequently using human-made structures as roosts. They feed mainly on small invertebrates and therefore seem dependent of natural habitat types, especially rich in vegetation and water (THOMAS 1988; WALSH and MAYLE 1991). Studies on bat communities inhabiting areas highly transformed by man, namely cities, showed that a relatively low number of species is adapted to live in densely built-up areas (JONES and JAYNE 1988; BENZAL and MORENO 1989). Urban bat communities compared with non-urban ones are characterized by a lower number of species, decreased species diversity, and a strongly expressed dominance of a single species (KURTA and TERAMINO 1992). However, there is little data on this subject and the variation of urban bat communities is still poorly known.

Typical urban species in this group of animals, which are absent or scarce in non-urban habitats, were not recorded. Inhabiting a variety of landscapes, bats show plasticity in space use. Up to now few publications have focused on the variability of foraging areas in relation to anthropogenic changes of the environment. It was pointed out that bat densities in a city are lower than in non-urban habitats. A longer period of foraging in the city is an effect of reduced insect abundance (GEGGIE and FENTON 1985; FURLONGER et al. 1987; KURTA and TERAMINO 1992; RYDELL 1992).

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So far there are no data showing the foraging sites and bat densities in a broader urbanization gradient – from the city centre through suburbs to the interior of a large forest. Therefore, the aim of this study was to determine the bats preference to different foraging areas in different landscapes and to conclude in what way it reflects the space use and bat community structure in the city and outside.

Material and methods

The study area covered lowland landscapes from the centre of a large city (Warsaw – about 2 million inhabitants) through its suburbs to the relatively undisturbed coniferous and mixed forest of the Kampinos National Park (Fig. 1). The Vistula river-bed, a few hundred metres wide, determined the north-east border of the study area. We divided the area into 5 urban zones, in the city: central (I) and outskirts (II), and outside of the city: suburbs (III), non-urbanized, close to the city – 15–22 km from the city centre (IV), non-urbanized far from the city – over 22 km from the city centre (V) (Fig. 1, Tab. 1). The central zone was located in densely built-up areas inside a historical centre where only some small areas were covered by residential houses and parks. The outskirts differed by relatively large areas covered by new residential houses (mostly multistorey, less than 30 years old). New low buildings dominated the built-up area of the suburban zone. The percentage of wooded area and arable fields was considerably higher compared to the city. Only villages occurred in non-urbanized zones (the border of 2 zones was arbitrarily determined taking into account the distance from city centre). The landscape was dominated by forests and arable fields.

The study was conducted between 1992–1994. Bats were recorded and counted by using an ultrasound detector (type PETTERSSON D 90 and D 100) along line transects 2 km long. In total 64 transects were surveyed (from 9 to 18 in each zone). We also classified them to 4 habitat types. Each transect represented one habitat type: wooded (forest or park), open area, built-up area, riparian.

Before starting the count we determined the atmospheric condition and selected only warm evenings (min. +15 °C but preferably > 20 °C), with little or no wind and no rain. Each transect was surveyed 3 times a season (in June, July, August). A single count lasted 2 hours starting with the calendar hour of sunset. During that time the transects were walked 3 times (each walk lasted 40 minutes). Bat records were mapped, and the following categories of behaviour were noted: (1) passes, (2) passes with foraging – we heard "feeding buzzes" or saw clear turns and changes in the height of flight, (3) circling with feeding. We also took note of the number of individuals (if we could see or hear many at the same time) and the species (if identified). Frequently it was too dark to observe bats, in some cases we did not know if we had heard the same or another individual (therefore we gave the number of records, not individuals). The next record (even if it was possibly the same individual already recorded) was noted after a break in bat calls of at least one minute. When bats were calling continuously, successive records were noted every two minutes.

During each count a detector was focused on 30–35 kHz, and after detecting a bat, the right frequency was found. The range of frequencies used by bats in the community studied was rather narrow – from 20 to 45 kHz. The species of bats were determined based on the rhythm, intensity and frequency of sounds, compared to records on the cassette (Ahlén 1989). We were able to identify 3 species. Bats of the genus *Myotis* were not distinguished, but taking into account their presence in roosts

Table 1. Number of transects under study in different habitats and zones (total 64).

Habitat type	Zone				
	Central (I)	Outskirts (II)	Outside city		
			Suburban (III)	IV	V
Built-up	6	8	4	4	3
Wooded	4	6	2	5	4
Open	0	2	2	4	3
Riparian	2	2	1	1	1

and results from netting (Kowalski and Lesiński 1995), probably the most common were *Myotis nattereri* and *Myotis daubentonii*, less frequently *Myotis brandtii* or *Myotis mystacinus*. Some records were not classified to species.

We described the intermediate surroundings of the transect within a 60 m wide belt (30 m on either side of the transect). If the habitat was not uniform, the transect was subdivided into sections not shorter than 200 m. We estimated the percentage cover of: trees, shrubs, open areas (crop fields, meadows, pastures, wasteland – if not in the range of tree canopy or shrubs), areas covered with concrete or asphalt, buildings, and waters. Also the number of working street lamps was noted.

Results

Relative density of foraging bats

The number of bat records on transects showed high variability within the urban zones (Fig. 1). Both transects rich and poor in bats occurred at each zone. The highest density of feeding bats was noted in a belt a few km wide along the river. Most bats in the city were recorded in riparian habitats, both in the central zone (2 records/100 m per count) and in the outskirts (1.3 records/100 m per count). Outside of the city the maximum bat densities were noted along the river (IV zone – 1.8 records/100 m per count) and in

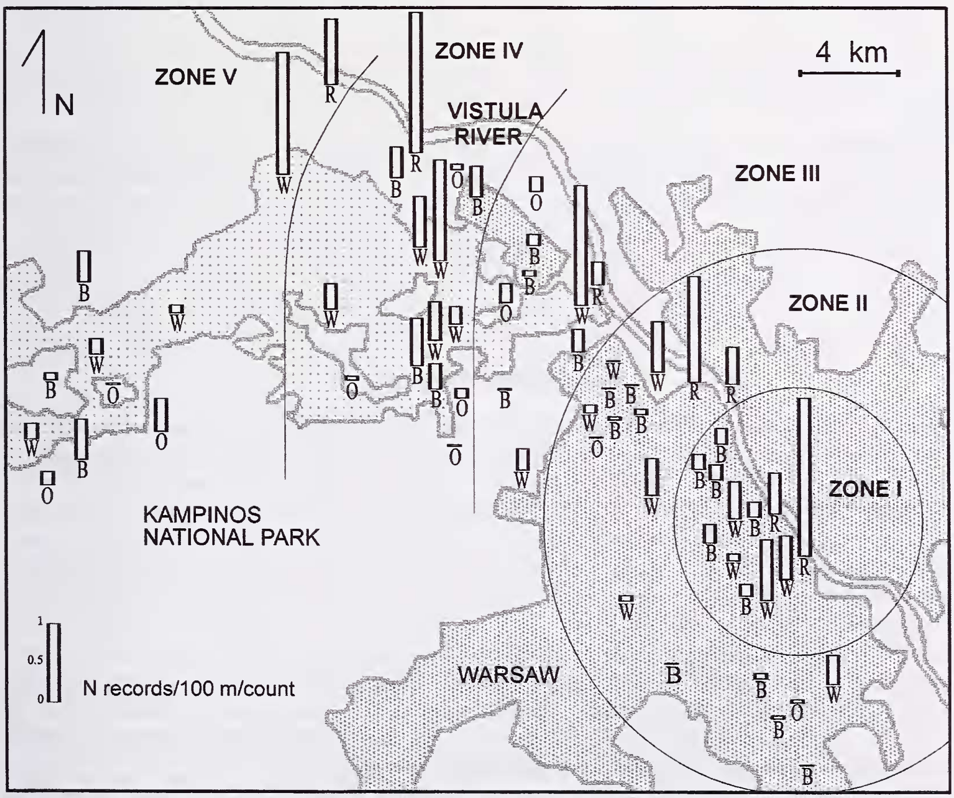

Fig 1. Total relative bat densities on transects within distinguished zones. I – central, II – outskirts, III – suburban, IV – non-urban close to the city, V – non-urban far from the city. Densely built-up area – dark grey, forests – light grey. Habitat type: O – open, B – built-up, W – wooded, R – riparian

wooded habitats: suburban zone III – 1.5 records/100 m per count, zone V – 1.6 records/ 100 m per count. Built-up areas in the city (especially the outskirts) were characterized by a low number of foraging bats (from 0 to 0.2 records/100 m per count). There were up to 0.5 records/100 m per count in the built-up areas outside of the city. The lowest number of bats was noted in open habitats. At 3 transects in the outskirts of Warsaw, located in open habitats, bats did not appear during all counts. Bats were rarely recorded also in open habitats outside of the city (up to 0.4 records/100 m per count at transects with relatively numerous trees).

Species composition of bats foraging in the city and outside of it

Eptesicus serotinus dominated the bats recorded by detectors in the whole study area. More than 60% of the records in the central zone dealt with this species. For many urban transects it was the only bat species noted. Its contribution in the community decreased with the decreasing level of urbanization. However, *Nyctalus noctula* and *Pipistrellus nathusii* were noted less frequently in the city. *Myotis* species densities were slightly lower in suburban and central zones, and higher further away from the city (Tab. 2).

Table 2. Total and percent of records represented by each species within the diverse zones. n – the sum excluding unidentified bats *Es* – *Eptesicus serotinus*; *Nn* – *Nyctalus noctula, Pn* – *Pipistrellus nathusii*

Zone	n	*Es*	*Nn*	*Pn*	*Myotis*
City					
Central (I)	334	66.5	28.4	1.2	3.9
Outskirts (II)	247	53.0	32.8	2.4	11.8
Outside city					
Suburban (III)	233	46.3	42.1	7.7	3.9
IV	409	46.2	34.2	5.4	14.2
V	222	43.2	29.3	3.2	24.3

Preferred bat foraging areas

The most numerous species, *Eptesicus serotinus* and *Nyctalus noctula* used each habitat type differently, both occurred less frequently in open areas (arable fields or meadows). The foraging of *Eptesicus serotinus* in a city was focused mainly on wooded and riparian habitats. The riparian habitat was rarely visited outside of the city (no more frequently than open areas), but the built-up area was as important as the forests. *Nyctalus noctula* was frequently noted in riparian habitats of all zones (up to 92% of records outside of the city), and rarely in built-up areas. The species frequently used wooded habitats in the city and suburban zone (Tab. 3).

The significant differences between *Eptesicus serotinus* densities in the city and outside of it were obtained in built-up areas and riparian habitats (Tab. 4). Also *Nyctalus noctula* foraged more frequently in riparian habitats located outside of the city than in Warsaw. Taking into consideration all detected species, the differences in preferred habitats outside of the city were noted for open and built-up areas.

The density of bats foraging over open habitats in Warsaw were significantly lower than in wooded and riparian habitats, both for *Eptesicus serotinus*, *Nyctalus noctula*, and all bat species. Regarding outside city zones, *Eptesicus serotinus* mostly foraged in wooded and built-up areas, and *Nyctalus noctula* distinctly preferred riparian habitats (Tab. 4).

For all bat species the least attractive hunting area was located in open habitats. Similar densities were noted in non-urban built-up areas and forests but were higher in a river valley compared to built-up and open areas. The highest density of an urban bat community occurred in parks and along the river (Tab. 4).

Among the 6 habitat characteristics described for the 60 m transect belt, five significantly influenced the density of detected species (Tab. 5). The percentage of shrub cover

Table 3. The use of different habitat types by *Eptesicus serotinus* (*Es*) and *Nyctalus noctula* (*Nn*) in urban zones (% of records per transect). x – no data, N – number of records

Zone	Species	N	Wooded	Built-up	Riparian	Open
City						
Central (I)	*Es*	222	47.1	20.6	32.3	x
	Nn	95	48.9	5.3	45.8	x
Outskirts (II)	*Es*	105	24.0	2.5	72.2	1.4
	Nn	49	17.2	2.2	78.0	2.7
Outside city						
Suburban (III)	*Es*	58	73.5	26.5	0	0
	Nn	41	29.9	6.7	52.2	11.2
IV	*Es*	154	44.1	45.7	6.2	4.0
	Nn	137	2.2	4.5	92.0	1.3
V	*Es*	96	41.4	41.4	6.9	10.3
	Nn	65	4.4	5.8	80.8	9.0

Table 4. Comparison of the relative densities of bats (number of records per 1 km of a transect) in different habitats in the city (central zone + outskirts) and outside the city. Median values (M), lower and upper quartiles (LQ, UQ) are given. Habitat type: O – open, B – built-up, W – wooded, R – riparian. Differences: NS – not significant, * – $p < 0.05$, ** – $p < 0.001$

Species	Habitat type	Non-urban habitats (1)			Urban habitats (2)			Differences 1 v. 2
		M	LQ	UQ	M	LQ	UQ	
Eptesicus serotinus	O	0.8	0	1.5	0.3	0	0.5	NS
	B	4.0	2.0	7.0	1.3	0	3.5	*
	W	5.0	0.8	11.0	8.0	1.0	9.5	NS
	R	1.0	0	1.0	6.5	3.0	13.0	*
Nyctalus noctula	O	1.0	0	1.8	0	0	0.5	NS
	B	1.0	0	3.0	0	0	0.5	*
	W	1.0	0.5	2.3	1.5	0.5	3.5	NS
	R	16.5	8.0	44.0	6.5	4.0	8.0	*
All species	O	2.8	1.0	5.3	0.5	0	1.0	*
	B	9.5	4.0	11.5	2.0	0.5	5.5	*
	W	13.0	6.3	23.3	12.5	2.5	16.5	NS
	R	25.0	10.0	51.0	16.0	13.0	25.0	NS

Differences between habitat types:
E. serotinus – non-urban: OB-*,O/W-*,O/R-NS, B/W-NS, B/R-*,W/R-*;
urban: OB-NS, O/W-*, O/R-*, B/W-NS, B/R-*, W/R-NS
N. noctula – non-urban: OB-NS, O/W-NS, O/R-*, B/W-NS, B/R-* *, W/R-*;
urban: OB-NS, O/W-*, O/R-*, B/W-*, B/R-**, W/R-*
All species – non-urban: OB-*, O/W-*, O/R-*, B/W-NS, B/R-*, W/R-NS;
urban: OB-NS, O/W-*, O/R-*, B/W-*, B/R-**, W/R-NS

Table 5. Correlation coeffcients between number of bat records and habitat characteristics of transects (% cover by different elements of habitat structure or number of elements per 100 m).
NS – not signifcant, * – p < 0.05, ** – p < 0.001

Habitat characteristics	*Eptesicus serotinus*	*Nyctalus noctula*	*Pipistrellus nathusii*	Total
Trees (%)	0.39*	NS	0.27*	0.51**
Open areas (%)	–0.38*	NS	NS	–0.45**
Waters (%)	NS	0.29*	NS	NS
Buildings (%)	NS	–0.39*	NS	–0.36*
Street lamps (n)	NS	–0.29*	–0.32*	–0.27*

Table 6. Correlation coeffcients between the number of bat passes without foraging or records of foraging bats and the habitat characteristics of transects.
Explanations as in table 4.

Habitat characteristic	*Eptesicus serotinus*		*Nyctalus noctula*	
	passes	foraging cases	passes	foraging cases
Trees %)	0.34*	0.39*	NS	NS
Open areas (%)	–0.34*	–0.40*	NS	NS
Waters (%)	NS	NS	NS	0.37*
Buildings (%)	NS	NS	–0.36*	–0.26*
Street lamps (n)	NS	NS	–0.32*	NS

appeared not to be significant in any case. The area covered by trees was the main factor for bats, especially *Eptesicus serotinus* and *Pipistrellus nathusii* (positively correlated with their densities). An increase in the percent of water showed increased *Nyctalus noctula* density. Working street lamps were not significant for bats or negatively correlated with the density of some species (*Nyctalus noctula* and *Pipistrellus nathusii*).

Separate analysis of passes without foraging and passes with "feeding buzzes" or clear turns (Tab. 6), showed that most of the obtained relationships were similar. Differences were noted in the case of *Nyctalus noctula*. The number of its passes did not correlate with the percentage cover of water. No correlation was found between foraging cases and density of working street lamps.

Discussion

Relatively low differences in bat density of comparable habitats within a city and outside of it indicate that urban habitats are only slightly less attractive for bats than non-urban ones. Many species find a variety of shelters in cities, and the main factor limiting their density seems to be the occurrence of trees and of water as resulted from this study. Vegetation obviously is especially important because potential bat prey is associated with trees or shrubs. Quantitative decreases in urban bat communities (Geggie and Fenton 1985) mostly depend on differences in the vegetation cover.

Eptesicus serotinus dominates the studied community because of its synanthropy and connection with anthropogenic shelters, both in winter and summer (Kowalski and Ruprecht 1984; Stebbings and Griffith 1986). The results of this study showed that feeding individuals of *Eptesicus serotinus* mostly fly near vegetation in parks and forests. Probably its numerous presence depends on the distance from shelters. For example, the riparian habitats were frequently visited in Warsaw (close to built-up areas with many lofts – preferred shelters) and rarely outside of the city. Nevertheless, comparatively long flights between shelters and foraging areas are known, usually up to 2 km (Glas 1980/81; Degn 1983), rarely more (Perez and Ibañez 1991; Catto et al. 1996).

The proportion of smaller species, e. g., *Pipistrellus nathusii* or *Myotis* spp. in the studied community could be higher than observed, because of the lower rate of detection (weaker sounds). However, even taking this into consideration, the dominance of *Eptesicus serotinus* is highly expressed, at least in urban habitats.

Our results confirm the high importance for bats of areas bordering on waters (McAney and Fairley 1988; Walsh and Mayle 1991; Rachwald 1992; de Jong 1994; Vaughan et al. 1997; Gaisler et al. 1998), both in the city and outside of it. Despite a lack of direct evidence, we can assume that in the study area *Nyctalus noctula* regularly flies between daily shelters in forests and foraging areas in the Vistula river valley. Also in Zürich this species frequently hunted on insects near the river (Stutz and Haffner 1985/86). Similar to our study area, cases of *Nyctalus noctula* foraging inside a forest were rather rare in the vicinity of Munich, but usually noted at forest edges and in open areas near a lake, up to 2.5 km from shelters (Kronwitter 1988). The lack of correlation between *Nyctalus noctula* passes without foraging and the percent of waters in the study area, indicates that in many cases these bats fly over nonspecific foraging areas whilst commuting.

Many studies have demonstrated the low importance of open areas for bats (McAnney and Fairley 1988; Gaisler and Kolibac 1992; de Jong 1994, 1995) and this was confirmed in Warsaw and the surrounding area. The lowest bat densities were noted in this habitat type independently from the level of urbanization. It can be explained by the lower abundance of potential prey (de Jong 1995), although not for all species of bats (Ekman and de Jong 1996), and perhaps also by a lack of linear landscape elements, that help bats to commute safely and make easier orientation possible (Limpens and Kapteyn 1991; Speakman 1991; Ekman and de Jong 1996).

Urban built-up areas appeared to be less attractive to bats than non-urban ones, this results from the low volume of vegetation among city buildings and generally lower densities of insects (Geggie and Fenton 1985; Jones and Jayne 1988).

Working street lamps have no distinct importance in bat foraging in the landscapes under study. Even the avoidance of sites with lamps were pointed out which contrasts with some data from western and northern Europe (Rydell 1991). Our study was carried out from June to August, therefore during the period of high insect activity. Working street lamps may be more important for bats in early spring and autumn when insects are less numerous and their local concentrations make foraging easier.

Results for *Eptesicus nilssoni* in Scandinavia also confirm this explanation. Until the first of May almost all individuals foraged near lamps but only 25–50% in June and July (Rydell 1991). Geggie and Fenton (1985) noted that foraging of *Eptesicus fuscus* near lamps occurred in non-urban habitats, and not in the city. Similar patterns were absent in the community under study.

For *Eptesicus serotinus*, feeding mostly on beetles (Robinson and Stebbings 1993), working street lamps are not attractive (those insects are not attracted to lamps). However, the negative correlation between *Nyctalus noctula* or *Pipistrellus nathusii* densities obtained here and the density of working street lamps was rather accidental. Both species are less numerous in urban habitats compared to built-up areas, where street lamps are common.

The results of this study have pointed out that detected bat species show different preferences for foraging areas. The described relationships, however, were not strict and explained rather a low percentage of variability in the observed bat densities. Probably it was because bats are opportunistic in foraging site selection and change habitats in relation to seasonal variation in the abundance of insects. This phenomenon has been shown for *Eptesicus serotinus* in southern England (Catto et al. 1996) and for the north American *Myotis yumanensis* (Brigham et al. 1992). *Eptesicus serotinus* can be identifed as best adapted to live in urban habitats of central Poland. *Nyctalus noctula* clearly penetrates the outskirts of Warsaw. *Pipistrellus nathusii* and some *Myotis* sp. show the highest level of avoidance of urban habitats.

Zusammenfassung

Jagdreviere und relative Dichte von Fledermäusen (Chiroptera) in von Menschen unterschiedlich veränderten Landschaften

Diese Studie über die Jagdreviere von Fledermäusen wurde auf 64 Transekten (je 2 km lang) in verschiedenen Habitaten und urbanen Regionen im zentralen Polen durchgeführt. Diesbezügliche relative Dichten von Fledermäusen in der Stadt (Warschau) waren nur wenig geringer als in vergleichbaren Habitaten außerhalb. Die höchsten Dichten ergaben sich für Baumbestände und Flußufer (in der Stadt: 2,0 und 1,0 Ortungen/100 m pro Zählung; außerhalb: 1,8 und 1,5 Ortungen/100 m pro Zählung). Offenes Gelände wurde von jagenden Fledermäusen am seltensten aufgesucht. Bebaute Regionen außerhalb der Stadt zeigten höhere Dichten als die städtischen. Die relativen Nachweise von *Eptesicus serotinus* waren im Zentrum der Stadt (mit ca. 66%) am höchsten und verringerten sich mit zunehmender Entfernung vom Stadtkern. *Nyctalus noctula* suchte in allen untersuchten Zonen hauptsächlich an Flußufern Nahrung. *Pipistrellus nathusii* und die Arten von *Myotis* waren häufiger in den weniger vom Menschen beeinflußten Landschaften zu finden. Baumbestände in den Jagdrevieren waren der wichtigste beeinflussende Faktor für die Fledermausdichte.

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